Cuttlefish interact with multimodal “arm wave sign” displays

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In addition to the well-known extraordinary changes in visual appearance they can generate at the level of their mantle, cuttlefish can produce various body configurations combining chromatic, postural, and locomotion patterns, both for camouflaging and communication. We introduce a previously undescribed communication display in two cuttlefish species: Sepia officinalis and Sepia bandensis. The four "arm wave signs" are stereotyped arm movements consisting of long-lasting, expressive, and repeated sequences of undulations of the arms, which can be combined and expressed following specific patterns. Using non-invasive behavioral experiments, we tested the hypothesis that they represent multimodal communication displays. To assess the role of visual cues, we recorded videos of animals signing and played them back to individual cuttlefish participants. When seeing the movies, cuttlefish waved back at the display. Most importantly, they were more likely to wave back when the movie was in upright (original) configuration as opposed to flipped upside-down, similar to the manner in which humans perceive faces and other socially relevant displays. In addition to their visually striking display, arm wave signs produce mechanical waves in the water, prompting us to explore the possibility that they may also be perceived via mechanoreception. Using playback experiments similar to those adopted in vision, we obtained preliminary evidence to support this hypothesis, indicating that arm wave signs may represent multimodal signals involving vision and mechanoreception. Our new result on communication with arm wave signs opens up novel possibilities for understanding vibration-mediated communication through the lateral line and/or the statocysts in a cephalopod species as an example of convergent evolution with vertebrates.

cephalopod cognition | cuttlefish behavior | multimodal communication | bioacoustics | playback method | vision | mechanoreception | lateral line | statocysts | convergent evolution

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Introduction

The cryptic abilities of cuttlefish, known as “chameleons of the sea”, are justly celebrated as stunning examples of animal camouflage. For example, Sepia officinalis can combine more than fifty body patterns to approximate specific features of artificial backgrounds (1–6). Skin patterning is a versatile ability that is also used for communication (7), the intense zebra bands being the most representative pattern during reproductive behaviors in Sepia officinalis (8). Cuttlefish can also use a variety of body and arm postures to communicate information about their intention to fight or mate (8). For example, the ’raised arms’ are associated with the ’flamboyant display’ to intimidate predators, while the ’extended fourth arm’ is used by male cuttlefish to communicate their intention to mate (7–9). Cuttlefish also alter the shape of their body: they can flatten their body to appear larger (9) and frighten a potential predator, as is the case in the deimatic display (7, 9, 10). More generally, arms can be "raised, lowered, splayed, split, V-curled, or contorted" as summarized by Mather (7). Arms can make the animal look larger and can be used to frighten and repeal as well as look more dominant.

Several functions have been suggested for behaviors that use arms in cephalopods, notably masquerade, flamboyant displays, and luring (7, 8). In cuttlefish and octopus, specific arm movements and postures have also been described and interpreted as mimicking behaviors. In cuttlefish, Okamoto and collaborators identified and studied a unique arm-flapping behavior in Sepia pharaonis to which they attributed the function of crab mimicry, especially during hunting (11). However, this study did not test the hypothesis that this remarkable display could also be addressed from one cuttlefish to another for communication. Norman had previously shown that arm postures and movements are used by octopus to mimic the behavior of sole, sea snake, and lionfish (12). However, as noted by the authors, there were no behavioral studies that complemented those findings to test the hypothesis of mimicry. In squids, communication through arm postures/movements and dances/choregraphies have been extensively studied and documented, notably in the form of ethograms (7, 13–15).

Cephalopods in general communicate multimodally by combining various sensory modalities: visually with body patterns (5, 16–21), via tactile stimulation (7, 22–24), chemically with ink or pheromones (25–31), and through light polarization (32–36). Cuttlefish do not have ears, but perceive sounds and low vibrations through their lateral line hair cells and their statocysts (10, 37–47). There is currently no clear evidence pertaining to the possibility that cuttlefish may interact with each other through sounds (to be understood as low-frequency vibrations) suh as vertebrate teleost fish or cetaceans (7, 48). However, it is established that they respond behaviorally to sounds ranging from 20 to 1000 Hz (38, 40–47, 49–52). The classical behaviors reported with sound stimulation are: startle response (53), inking, jetting, and rapid coloration change, moving, burrowing, orienting, swimming, and body patterns associated with specific frequencies such as dark flashing, bleaching, and deimatic display (40, 41, 43, 44, 51, 54). In squids, several escape responses (inking, jetting, fleeing, deimatic dis-

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play) evoking predator evasion have been revealed (55). As Mather stated, despite the lack of evidence so far, it is possible that cephalopods can detect vibrations created by conspecifics using the lateral line to facilitate social behavior, shoaling at night (7). To our knowledge, there is currently no evidence of communication through arm movements that would be perceived by mechanoreception (sound/vibration) in cephalopods.

In amphibians and fish, the lateral line is involved in prey detection, predator avoidance, rheotaxis (56), the localization of stationary objects, and schooling behavior (57, 58). It also provides a sense of spatial awareness for the animal and participates in its ability to navigate the surrounding environment. Evidence from comparative ecology in fish and amphibians, which are the two other groups equipped with a lateral line organ, supports the notion that the lateral line plays a role in communication (59–63). The cuttlefish lateral line and statocysts are an example of convergent evolution between an invertebrate and a vertebrate sensory system (37, 45). In cuttlefish, the attested function of the lateral line is the detection of small movements of water conveyed by hydrodynamic pressure gradients (37, 39, 64, 65). Cephalopods can perceive long-range sounds through their statocysts, particle-motion detectors (43) akin to the cochlea in vertebrates (41, 42, 45–47, 50). In cephalopods specifically, the function of the lateral line and the statocysts has been established for navigation, detection of prey, predator avoidance, and, hypothetically, social schooling behavior (39, 66, 67).

In this study, motivated by the evidence reviewed above, we report a previously undescribed category of arm wave displays in two species of cuttlefish (Sepia officinalis and Sepia bandensis), which we refer to as "arm wave signs" (**Figure 1**, **Supplementary Videos 1–4**). We hypothesized that those signals are communication displays that cuttlefish use to interact with each other due to their specific features. The four "arm wave signs are stereotyped arm movements consisting of repeated, expressive, long-lasting sequences of undulations of the arms, which can be combined and expressed in correlation with other body patterns, including classically described dynamic skin body coloration for communication.

After presenting specific ethograms of the signs in two cuttlefish species, we present the results of two non-invasive behavioral experiments. First, we tested the hypothesis that these arm movements are informational displays used by cuttlefish to interact with one another visually. Our setup consisted in randomly presenting to the cuttlefish videos of themselves signing in upward (normal) and upside-down (control) configurations.

Prompted by the results obtained in the visual domain, we tested the hypothesis that arm waves may be perceived via mechanoreception, given that they produce mechanical waves in the surrounding water. The lateral line and the statocysts are the two candidate organs in cuttlefish for the perception of low-frequency movements generated by the arm wave signs (37, 39). We recorded traces of arm wave displays with a hydrophone (for the common cuttlefish) and a speaker (for juvenile Sepia bandensis) and played the traces

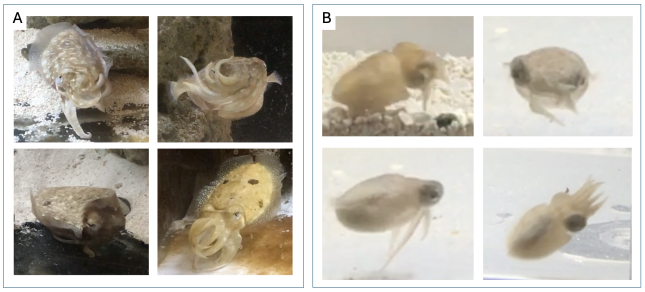

Fig. 1. The four arm wave signs in adult Sepia Officinalis (A) and juvenile Sepia bansensis (B)-**A1**-The "up" sign, most frequently expressed, has a distinctive feature of extension of the first pair of arms in the vertically upward direction of the head and the extension of the fourth arm pair, while the second and third arm pairs are twisted in the middle. **A-2**-When expressing the "side" sign, cuttlefish enroll all the arms on one side or the other of the body. **A-3**-The "roll" sign consists in enrolling completely all the arms beneath the head, changing the shape of the later and making the eyes appear prominent. **A-3**-At last, the "crown" sign consists in a movement of 'spitting' while all the arms are arranged in a crown shape. Cuttlefish exhibit the wave signs in different behavioral contexts (**A-1–3–4**-sitting), **A-2**-swimming, different orientations (**A-1–2–4**-frontal), **A-3**-with laterality, alongside with expression of highly contrasting skin patterns (black points in **A-3**-vivid orange color and black spots in **D4**) and **A-3**-contractions of the fins. **B**-The variant of the 'up', 'side', 'roll' and 'crown' sign in juvenile Sepia bandensis. See **Supplementary Videos 1-4, 5.**

back to the animal in normal configuration as well as two control configurations (reversed and scrambled). The playback method has been widely used in ethological studies as a way to project back a sound of communication to an animal and record their behavioral responses (68, 69). Several studies have investigated the behavioral responses of cephalopods to sound projected by underwater speakers, and have shown that statocysts perceive particle acceleration (40–42, 47, 51, 54, 70). To our knowledge, our study is the first to introduce hydrophone/speaker-mediated playback as a method to induce specific arm movements in cuttlefish.

Below we first present results from the non-invasive behavioral experiments introduced above, which provide the first evidence that arm wave signs may represent communication signals perceived visually and through mechanoreception. In the discussion section, we address the implications of our study for the study of communication through arm movements in cephalopods. We finally open the debate on the potential role of the lateral line and statocysts in perceiving arm wave signs in cuttlefish, and the possible function of mechanoreceptors in communication behavior as an example of convergent evolution between cephalopods and vertebrates.

Methods

A. Animals and husbandry. We conducted two types of behavioral experiments. For the first 'visual experiment', we tested eight adult cuttlefish Sepia officinalis (3-12 months) and ten juvenile cuttlefish Sepia bandensis (1-2 months). For the second 'playback experiment', eight adult Sepia officinalis cuttlefish and eight juvenile Sepia bandensis cuttlefish were tested. All animals were reared from eggs and kept in

hatchlings following established guidelines (71), at the authorized institutional supplier Aquarium de la Rochelle (La Rochelle, France). The eggs were collected in the Atlantic Ocean (for Sepia officinalis) or in the Indo-Pacific Ocean (for Sepia bandensis). The cuttlefish were reared in captivity (hatched from the eggs) by a team of biologists specialized in the breeding of cuttlefish. Transportation was optimized by oxygenation enrichment, noise and vibration minimization in a cool specialized container without light exposure, and following food deprivation prior to transport to avoid accumulation of toxic ammonia level. Once the eggs / juveniles reached our facility, they were acclimatized in four artificial marine water tanks (300 L each) for 2 hours. When handling eggs, we introduced additional air pumps to provide sufficient oxygenation for their development.

We ensured that the environment of all four fiberglass tanks (300 L each) approximated the natural habitat as closely as possible while providing adequate monitoring of water quality and animal health and well-being. The tanks operated a closed-water system that allowed constant monitoring and optimization of water parameters and contained various oxygen pumps, a skimmer, mechanical and biological filtration, and carbon for ink removal. We introduced sand enrichment (7-cm layer of natural marine uniform sand with granulometry of 1–4 mm, enriched with natural pebbles of different size/color placed randomly across the tank), and live rocks ($\sim$15 live rocks of different sizes for a total of $\sim$20 kg per tank) to provide shelter, and more generally to encourage cuttlefish expression of their full behavioral repertoire (burying in sand, establishing territories and dominance hierarchies, protection from lighting within areas shadowed by rocks, swimming by jet propulsion).

The tanks were visually isolated from each other to prevent cuttlefish from interacting with animals in other tanks, and the tank surfaces were opacified with adhesive vinyl sheets to minimize mirror reflections. We established a light/dark cycle of 12 hours / 12 hours and only conducted experiments during the day. Live food was provided three times a day: at 9 a.m., at 2 p.m., and at 8 p.m. We never deprived animals; instead, food was systematically provided so that cuttlefish could hunt at will (especially at night) and would not engage in aggressive behavior for food competition. From hatchlings to 1 month of age, cuttlefish were fed a mixture of live Artemias and live Mysids. Once they reached 1 month of age (2 month for Sepia bandensis), they were fed larger live grass marine shrimp (*Palaemonetes vulgaris*) and live crabs.

B. Ethical Statement. In this study, we performed two types of non invasive observational experiments: visual and playback experiments. None of these two experiments involved an invasive procedure, pain, or lasting harm to the animal. In order to respect the 3R's principles (72) and following established guidelines for the use and care of cephalopods in captivity (71), we provided the animals with large tanks enriched with sand, rocks, sheltered area and gave only live food at will to allow expression of their full behavioral repertoire, notably hunting at will (Refine). We allowed a maximum of six animals per tank. We managed to establish a trade-off between sufficient statistical power and reduction of the number of animals used per experiment (Reduce). Our observational non-invasive experiments are therefore classified below the threshold for explicit ethics approval as expressed in Directive 63/10. However, we searched and obtained validation from the head of the ethic commitee of our Biology Department (IBENS, École Normale Supérieure, Paris, France).

C. Experimental procedure.

C.1. Visual experiment. Visual stimuli and presentation protocol.

Our first goal was to record sequences of spontaneous expression of the four arm wave signs in a variety of behavioral contexts. When a cuttlefish settled or moved, signing, within a specific area of its choice, we placed an underwater camera (GoPro Hero13) above the tank to record the mantle $\sim$2 hours, three times a day, for a period of $\sim$9 months. To obtain frontal video footage of the face and arms, we placed an iPad Pro Retina (iPad Pro Retina 12.9) in front of the tank to record cuttlefish waving from a standardized point of view. To construct our stimuli, we selected sequences of signs for each individual, over several months (1-7 months) to collect a large dataset in various orientations to the camera view point, with several body pattern associated (See **Supplementary videos S5**). We then randomly selected sequences from this dataset where the cuttlefish elicited the wave signs, spaced by sequences where they did not. For the Sepia officinalis cohort, we presented a stimuli movie displayed on the black background of a MacBook Pro 13" screen (Intel Iris, 2GHz Intel Core-i running on MacOS Sequoia 15.3.2) with window size: 0.50. We generated 18 sequences presenting 6 males and 7 males (aged 3-7 months) intercalated with presentation of cuttlefish not signing. In total the stimuli video combined 61 signs and lasted 10 minutes. We randomly presented the normal version and a control presenting a flipped version of the video (upverted condition).

For the Sepia bandensis cohort, we selected four versions of arm wave signs (two versions of the "up" sign and two versions of the "crown" sign). We created a flipped version of those videos. In addition, we added two other control categories: non-signing (two with cuttlefish standing still, two swimming) and non-signing upverted (See **Supplementary videos S7**). We generated a custom Python script that randomly picked up one video of each of the four categories: 'signing', 'signing flipped', 'no sign', 'no sign flipped' and displayed them randomly with the VLC software (VLC version 3.0.21 for MacOS) on the black background of a MacBook Pro 13" screen (Intel Iris, 2GHz Intel Core-i running on MacOS Sequoia 15.3.2), with window size: 0.60, for 20 minutes. Each version of the stimuli lasted 5 seconds and a pause video constituted by a video of the empty tank was intercalated between each stimuli video. Our Python script automatically recorded the random sequence displayed with timestamps for future data analysis. We presented both movies and their controls during sessions of 5-10 trials a day, over a period of 1 month. We tested on average three randomly se-

lected animals placed in the testing arena tanks per day during sessions lasting two hours maximum to prevent both animal fatigue and habituation. Before testing, we let each animal acclimate for thirty minutes to the test tank to prevent any biais due to stress. No particular conditioning or reinforcement (e.g rewarding) was performed. We allowed breaks between each trial to allow the animal to rest and prevent early habituation to stimulation.

C.2. Playback experiment.

Construction of the playback stimuli Our second goal was to record sequences of spontaneous expression of wave signs in a cuttlefish Sepia officinalis (eight months) and a juvenile Sepia bandensis (1 month) that we would then playback to our test animals. To record the vibrations emitted by the arm waves, we used a hydrophone Brüel and Kjaer Type 8103 for Sepia officinalis and Aquarian Audio hydrophone model AS1 Scientific for Sepia Bandensis both connected to an amplifier. The hydrophones were connected to a MacBook Pro (Intel Iris, 2GHz Intel Core-i running on MacOS Sequoia 15.3.2) through an interface. We captured the traces with the online software Audacity (c). Additionnally, we used the Zoom F3 recorder connected to the Aquaria AS1 hydrophone. We isolated seven instances of the 'up' wave sign, each cropped to 10 seconds in the first case, and eight instances of the 'up' and 'crown' sign in the second case lasting each 5 seconds. The 10 and 5 seconds were chosen according to the maximum average lasting of a sign in Sepia officinalis and Sepia bandensis respectively. For each instance, we generated two control waveforms: reversed and scrambled. The "reversed" waveform was obtained by simply time-reversing the original trace. This manipulation is relevant because it can lead to a loss of interpretability for meaningful sounds, while largely preserving the low-level content of the original trace. For example, speech becomes unintelligible when played backwards (73, 74). To obtain the "scrambled" waveform, we computed the Fourier transform of the original waveform, replaced its phase spectrum with one obtained from a random trace in which each time point was randomly assigned a value from a Gaussian distribution, and then computed the inverse Fourier transform to obtain the corresponding waveform. In this manner, the scrambled waveform retains the same power spectrum associated with the original waveform, but loses the original phase structure. This manipulation is interesting because it removes important features of natural signals, while preserving the amount of overall intensity associated with the original stimulus. For example, interference with the power spectrum of natural scenes causes a little drop in recognizable content, provided the phase spectrum is left unaltered. In contrast, interference with the phase spectrum renders the content of natural scenes uninterpretable, even though the power spectrum may have been left unaltered (75). We then generated a pseudo-random sequence of the three stimuli detailed above: an initial pause of 10 seconds, followed by a stimulus, another 10-second pause, another stimulus, and so on, for a total of 21 stimuli over a period of approximately 7 minutes (430 seconds). Each stimulus was randomly selected

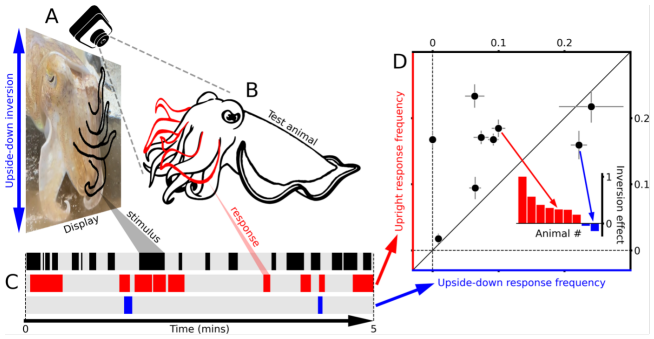

Fig. 2. Cuttlefish Sepia officinalis wave back at movies of other cuttlefish waving. A Footage of cuttlefish producing wave signs was played back to a real cuttlefish **B** looking at a flat screen, while the animal was being simultaneously recorded (camera in **A**). This setup made it possible to align occurrences of wave signs in the visual stimulus (indicated by black segments in **C**) with occurrences of wave signs produced by the test animal (indicated by red segments in **C**). As indicated by the 5-minute excerpt in **C**, it appears that the test animal produced wave signs in response to those delivered by the visual stimulus, possibly with some delay. Furthermore, when the visual stimulus was inverted upside-down during playback (blue double-headed arrow in **A**), the test animal produced fewer signs (blue segment in **C**). We quantified this effect by calculating the frequency of signing in the upright configuration, plotted on the y axis in **D**, versus the frequency of signing in the upside-down configuration, plotted on the x axis in **D**, separately for each animal (one data point per animal). Data points that fall above the diagonal unity line indicate more frequent response in the upright configuration compared with the upside-down configuration, while points that fall below the diagonal unity line indicate the opposite trend. To further quantify potential differences between upright and inverted configurations, we computed their normalized difference (see main text) in the form of an inversion effect, plotted in the inset to **D**, separately for different animals. Error bars in **D** plot ±1 SEM.

to be the normal waveform, the backward waveform, or the scrambled waveform in such a way that each waveform type was presented seven times during the 7-minute sequence.

Set up of the behavioral experiment Our experimental objective was to playback with a hydrophone the constructed stimuli to our 8 cuttlefish participants Sepia officinalis. We also aimed to design a variant of the playback experiment with Sepia bandensis using an underwater speaker equipped with subwoofers. To test the cuttlefish Sepia officinalis, we did not interfere with their daily routine. We let the animals evolve naturally in their home tank to encourage the expression of natural and spontaneous behavior. We waited for a cuttlefish to settle in a specific area of its choice and tested the animal when the hydrophone (Brüel and Kjaer Type 8103) was at a distance of approximately 3-10 cm from its arms (one body length for adult cuttlefish Sepia officinalis). An underwater camera (GoPro Hero7) was also fixed in advance above the tank to record the mantle and collect data of the correlated expressed dynamic skin patterns. For Sepia bandensis, we designed a variant of the setup and completely isolated the animal in a specific test tank. We randomly picked a juvenile cuttlefish from the home tank and let the animal acclimate in the new tank for 30 minutes prior to testing to prevent any biais due to stress. The speaker (Ortizan X8 Pro or TOZO PA1), enclosed in a thin waterproof bag for better water protection, was already settled in the test tank in advance to prevent the animals from stressing with the introduction

of an object that could be mistaken for a predator. For both experiments, the display of the stimuli was controlled with a custom Python script running on a MacBook Pro (Intel Iris, 2GHz Intel Core-i running on MacOS Sequoia 15.3.2) ensuring the playback of the pseudo-random sequence both for the hydrophone and the underwater speaker. Our code saved the sequence displayed for each trial for further blinded analysis. We placed an iPad Retina Pro and a camera GoPro Hero13 (in front and above) the settled participant to record the responses of the cuttlefish to the stimuli.

C.3. Data Analysis.

Visual experiment For Sepia officinalis, we carried out 10-15 trials per day for a period of 2 months and collected 128 trial-associated video recordings in 8 cuttlefish (aged 8-12 months). For Sepia bandensis, we carried 10-15 trials per day for a period of 1 month and collected 52 trials for 10 animals (aged 1 month). To analyze the trials videos for both Sepia officinalis and Sepia bandensis, we considered each video and analyzed it individually. To label the production of response wave sign to the stimuli, we opened each video and manually annotated the production of the wave sign of each video in a text file with the corresponding timestamps. Labeling was performed blindly. It was not possible to know the nature of the delivered stimuli. Instead, we had written a custom Python script that saved as log text files the timestamps of each sign displayed randomly for automatic matching with the labeled text files.

Playback experiment For Sepia officinalis, we carried out 10-15 trials per day for a period of 3 weeks and collected 113 videos associated with the trials in 8 cuttlefish (aged 8-12 months). For Sepia bandensis, we carried 10-15 trials per day for a period of 2 weeks and collected 49 trials for 10 animals (aged 1 month). To analyze the trials videos for both Sepia officinalis and Sepia bandensis, we considered each video and analyzed it individually. To label the production of response wave sign to the stimuli, we opened each video and manually annotated the production of the wave sign of each video in a text file with the corresponding timestamp. During the annotation process, it was not possible to know the nature of the stimulus delivered to the animal at a given point in the video, both because the stimulus sequence was randomized (see above) and because the experiment did not involve any visual stimulation, meaning that the video recordings did not carry any direct information about the stimulus delivered by the hydrophone or speaker. For each trial, our custom Python script saved as '.npz' files the type of stimuli delivered (normal as 0, control as 1, scrambled as 2) with associated timestamps for future automatic matching with the labeled text file. For the cuttlefish Sepia officinalis, we also collected data on skin body coloration expressed during the playback experiment with a GoPro (GoPro Hero 7) camera mounted above the tank. We manually annotated the expression of strong highly contrasted skin body coloration patterns. We annotated as communication displays those instances in which

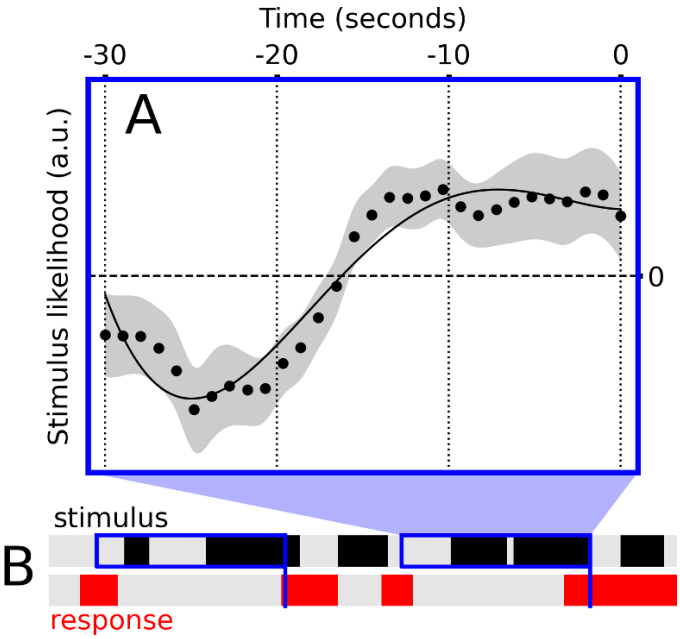

Fig. 3. Cuttlefish Sepia officinalis respond to visual wave signing in sluggish fashion over several seconds. We computed the behavioral equivalent of a spike-triggered average: for each occurrence of a wave sign produced by the test animal (indicated by **B**), we extracted the preceding 30-second binary sequence of visual stimulation (absent/present of wave signing in the visual stimulus, indicated by black segments in **B**). This procedure is indicated by the blue elements in **B**: a time point is selected within the red segments, as indicated by blue vertical lines in **B**, and the preceding 30 seconds of the stimulus are extracted, as indicated by blue rectangles in **B**. We then averaged across all extracted 30-second segments to produce the trace in **A**. This trace was computed separately for each experiment, and we subtracted its mean across time separately for each experiment to normalize its baseline to 0. **A** shows the average across all experiments and animals. We did not measure substantial differences between upright and inverted traces, so we show the combined case here. Zero on the x axis indicates the production of a wave sign on the part of the test animal. The trace in **A** shows that this response is triggered by stimulation occurring over an extended period of 15 seconds before the event, indicating that test animals do not respond immediately to the sight of a wave sign, but rather integrate the stimulus over several seconds before producing their response. This information was integrated into the analysis that went into **Figure 2D**

the color/brightness of the body pattern changed vividly and rapidly. For example, we would label a time window in which the cuttlefish would exhibit a bright orange pattern or a vivid black point in response to playback stimuli. We took as a reference the coloration classically referenced as skin body coloration displays in the literature on cuttlefish Sepia officinalis (2–9, 21, 76).

Statistical analysis. For both experiments, we carried out ANOVAs, t-tests, Wilcoxon tests, and Friedman tests and plotted the figures with custom Python script and Prism 10 (Version 10.4.1) software.

Results

Ethograms of the four arm wave signs. Extensive observations over several months on two successive colonies of 24 cuttlefish Sepia officinalis animals led to the identification of four stereotyped 'arm wave signs' displayed in differ-

ent behavioral contexts. (**Figure 1**). They are long-lasting movements of the arms lasting between 2-10 seconds, exhibited in repetitive sequences where different signs can be combined with other signs. Those arm waves signs that we call “up”, “side”, “roll” and “crown” are lateralized and can be expressed in all orientations to the viewpoint. They can be combined with the expression of various communication chromatic body patterns and locomotor components such as the undulation and contraction of fins (**Figure 1A**). They can be expressed by both juveniles and adults, males and females. We observed that they can be displayed to other cuttlefish, prey, and humans. In addition to being expressed during interactions between cuttlefish themselves, they are associated with various behavioral states: spontaneous states that do not involve specific sensory stimulation, while swimming, during the eating period, and while resting and burying. They can be expressed while hunting for prey. They are expressed as an aversive signal in occasion of introduction of an object in the tank (e.g a net). We postulated and experimentally tested that these arm waves are an intraspecific communication signal used by cuttlefish to interact with each other. They appear as ’supernormal stimuli’ costly in terms of fitness, which contrast with a possible camouflaging function due to their high visibility and attractiveness, exaggeration (77, 78). Since every cost comes with a trade-off, those wave signs must be beneficial to the animal in terms of fitness, for instance, if they use them to convey useful information (for reproduction, for instance).

In Sepia bandensis (**Figure 1B**), we identified the existence of a variant of these four signs. Especially, the "up" and "crown" signs are frequently expressed by the animals, from very early juvenile stages (1 week). The "crown" sign appears as a defensive display in these juvenile cuttlefish as well as the ’roll’ sign. The crown sign is often repeated several times in a row and is associated with dark skin coloration.

The arm wave signs are perceived visually and elicited by a visual playback display of their own signs. We performed the visual experiment on two distinct cohorts of cuttlefish. A first complete ’visual experiment’ was performed on 8 adult cuttlefish Sepia officinalis. A second complete similar version of the visual experiment was slightly adapted to test 10 juvenile Sepia bandensis. For the first experiment, Sepia officinalis were individually tested in front of the visual stimuli display consisting of videos of themselves displaying a random sequence of arm wave signs. We measured the probability of responding by wave signing, for all cuttlefish in the same time window to the presented normal and inverted version of the stimuli (**Figure 2A**). In the scatter plot (**Figure 2D**), each dot represents an animal participant. We can visualize the frequency of signing during epochs when the visual stimulus displays wave-signing actions (indicated by black segments in **Figure 2C**). Our measurements show a tendency to fall above the diagonal line, indicating that signing was more frequent in the upright configuration compared to the inverted configuration. To further quantify this effect and test its statistical significance, we computed the normalized difference between upright and inverted configurations

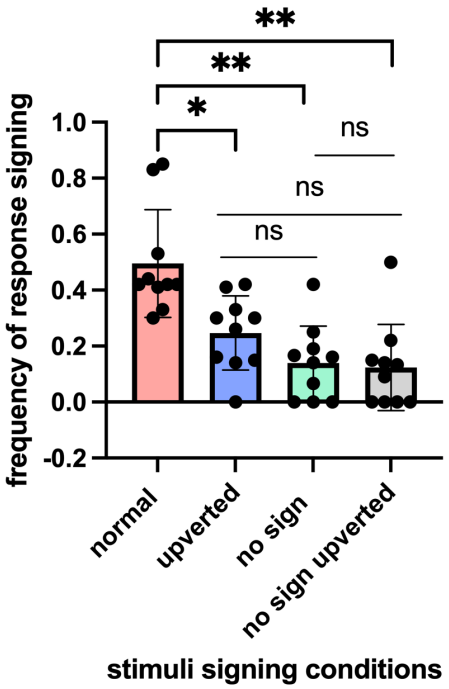

Fig. 4. Sepia bandensis wave back at movies of themselves waving "up" and "crown". On the bar plots, each dot represents an animal. Each bar represents the frequency magnitude of signing back at the visual display for the four different conditions.

in the form of (y-x)/(y+x), where y is the value on the y axis and x is the value on the x axis in **Figure 2D**) This index, which we term the “inversion effect,” is 1 if animals only sign for the upright configuration (x=0), 0 if they sign equally for both configurations (y=x), and -1 if they only sign for the inverted configuration (y=0). As shown in the inset to **Figure 2D**, the inversion effect shows a tendency towards positive values between animals, as confirmed by a Wilcoxon test for these values to differ from 0 ($p < 0.02$)**.**

When computing frequency of signing in **Figure 2D**, it was necessary to take into account the stimulus-response delay involved in the signing process: Even before running the experiment, we knew that cuttlefish would not sign back at the visual stimulus immediately because, at the very least, they would need time to process such a complex stimulus and initiate a corresponding motor response on their own part. In other words, it would be unrealistic to expect that the red segments would perfectly align with the black segments in **Figure 2C**, even for noiseless measurements of a perfectly responding system. To estimate the delay involved, we performed a behavioral variant of the spike-triggered analysis used in electrophysiology to characterize the temporal impulse response of sensory neurons (see caption to **Figure 3** for details). Using this approach, we identified a sluggish response spanning approximately 15 seconds of temporal integration (positive portion of the trace in **Figure 3A**). We then incorporated this knowledge into the analysis presented in **Figure 2D**: before computing the signing frequency during stimulation epochs, we convolved the stimulus trace with a 15 second temporal integration window that effectively de-

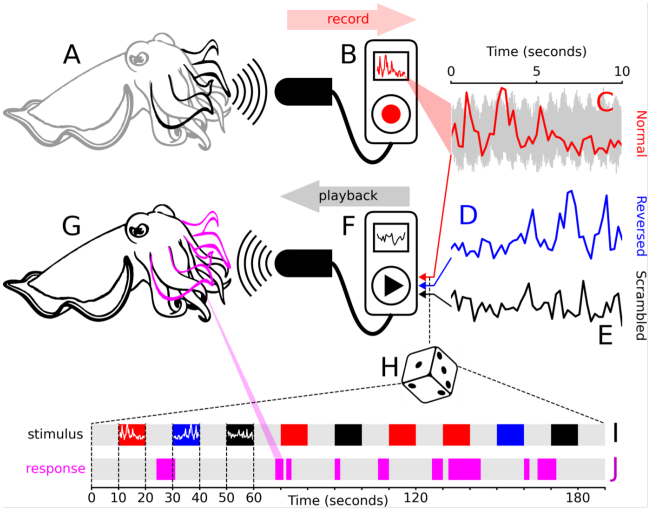

Fig. 5. Experimental design for studying wave sign production in response to mechanosensory stimulation with a playback display. To create our stimuli, we recorded the pressure waves created by cuttlefish **A** by placing a hydrophone **B** in the vicinity of their tentacles during wave signing. To visualize relevant structure contained within the recorded trace, we have superimposed onto the original recording (gray trace in **C**) a plot of power within the range 10–30 Hz (red trace in **C**; see also **Figure 8**. For each sample of the wave sign, we created two additional stimuli: a reversed stimulus **D**, obtained by simply time-reversing the original trace, and a scrambled stimulus **E**, obtained by randomly scrambling the phase spectrum of the original trace while preserving its power spectrum (see main text). We then played back these stimuli in pseudo-random order (**H**–**I**) to a test animal in the tank (**F**–**G**), and recorded wave sign responses from the test animal using the same procedures adopted in **A**. During stimulation, each stimulus (indicated by colored segment in **I**) lasted 10 seconds, followed by a 10-second pause (indicated by gray segments in **I**), and then the next stimulus. Color coding in **I** corresponds to **C**–**E**: red for the original (normal) trace, blue for reversed, and black for scrambled. We video-recorded the test animal to identify instances of sign production (magenta in **G**–**J**), which could then be matched against the stimulus sequence **I**–**J**.

layed and smeared the stimulus sequence in accordance with **Figure 3A**.

We sought to validate and reproduce the results obtained from our first experiment on Sepia officinalis on a different species of cuttlefish, Sepia bandensis, in a younger age stage, displaying comparable arm wave signs **Figure 1B**. During this second experiment, ten cuttlefish were individually placed in a test tank in front of the video stimuli display. The animals showed a similar significant and robust tendancy to sign more frequently to the upright configuration rather than to the upverted control and the non-sign and non-sign upverted conditions (**Figure 4**). This effect was confirmed by a repeated measured one-way ANOVA against the 4 conditions **(p=0.0007)**, corroborated by a two-tailed paired t-test between condition upward and flipped **(p=0.0147)**, upward versus no sign **(p=0.0040)**, upward vs no sign flipped **(p=0.0036)**. No significant effect was found between upverted, no sign, and no sign flipped.

Cuttlefish wave back at a vibratory playback of their own arm wave signs. We recorded the traces of the "up" sign (Sepia officinalis) and "up" and "crown" sign (Sepia bandensis) with a hydrophone. We then played back the filtered

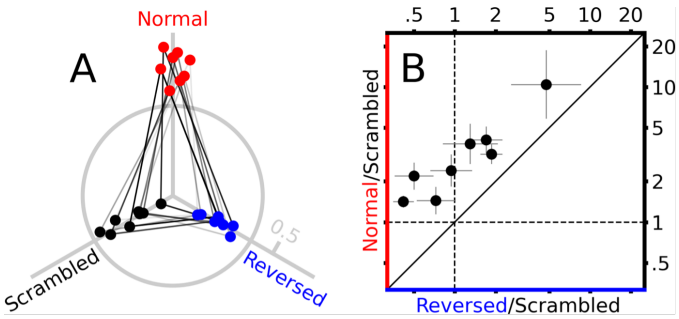

Fig. 6. Cuttlefish Sepia officinalis sign more significantly to the normal version of the played back arm wave trace. **A**–**B**: Distance circle **A** and scatter plot **B** representing the frequencies of signing for the three conditions. Each dot represents an animal.

traces with both a hydrophone (first case) and a speaker (for the second species). Our aim was to test the hypothesis that signs, provided that they create mechanical waves in the water, would be perceived by mechanoreception for communication. In this section, we present the results supporting that the low-frequency vibrations, corresponding to the traces of the wave signs, elicit the expected wave sign response in the two species of cuttlefish. We studied the probability of signing for each animal in response to the three waveform types: normal, reversed and scrambled. **Figure 5** is an illustration of our experimental setup. **Figure 5I** shows a 3-minute sequence during which the three types of stimuli are played in pseudo-random order. **Figure 5J** shows example responses in one animal: magenta segments indicate instances of sign production on the part of the test animal in response to the stimulus sequence in **Figure 5J**. By comparing the stimulus and response sequences, we can measure the probability of signing for the different types of stimulus events. **Figure 6A** plots the resulting probabilities of signing for each animal (each data point) and for the three different types of stimulus (different spokes). The frequency magnitude is reflected by the distance from the center of the plot. The gray circle represents an equal frequency of approximately 0.4 in the three stimulus configurations. The data points for the normal configuration (red in **Figure 6A**) lie outside the circle, which means that the sign frequency for this configuration is greater than 0.4. The data points for the other two configurations lie inside the circle, which means that the associated signing frequency is smaller than 0.4. In other words, animals sign more in response to the normal waveform when compared with reversed/scrambled waveforms. To confirm the significance of the data pattern suggested by the visualization in **Figure 6A**, we followed a Friedman test to determine whether there was any difference in signing frequency across the three conditions, and obtained $p < 0.003$. We then proceeded with a Conover post-hoc test to evaluate pairwise differences between conditions (corrected for multiple comparisons), which returned significant differences ($p < 0.01$) for normal-versus-scrambled and normal-vs-reversed, but not difference ($p = 0.35$) for scrambled-versus-reversed. If we take the scrambled configuration as baseline reference, and express frequency values for the other configurations as ratios to the scrambled configuration, we find not only that the nor-

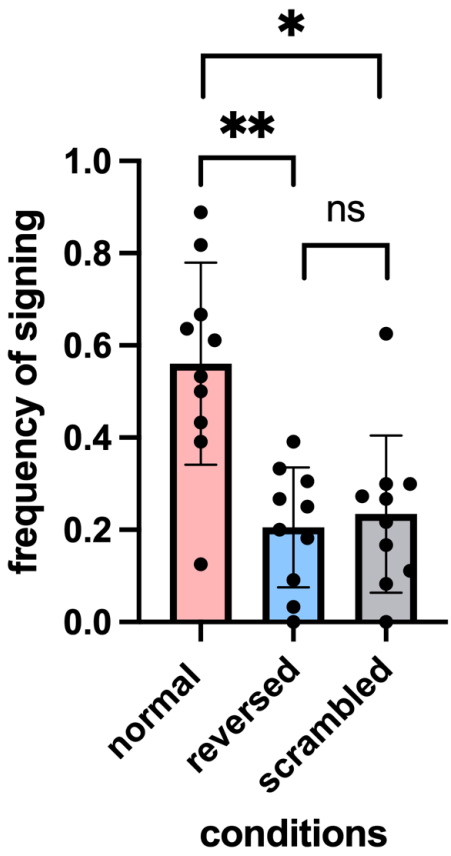

Fig. 7. Playback of the wave sign elicit arm wave sign response in Cuttlefish Sepia bandensis. On the bar plots, each dot represents an animal. Each bar represents the frequency magnitude of signing back during playback with a speaker for the three conditions (normal vs two controls, reversed and scrambled) .

mal configuration is associated with larger normalized values than the reversed configuration in a one- to-one comparison across animals (data points fall above the unity line in **Figure 6B** at $p < 0.01$ on a paired Wilcoxon test), we also find that these two quantities are strongly correlated (Pearson's $r = 0.93$, $\mathbf{p} < 0.001$). The latter result demonstrates that, when appropriately normalized to a common baseline, our dataset is internally consistent across animals.

In Sepia bandensis, we were able to reproduce the playback experiment with an underwater speaker and studied the probability of signing for each animal in response to the three waveform types. The normal played back trace was a random instance of the "up" or "crown" sign previously sampled from a juvenile of the same colony with a hydrophone.

Nine out of ten animals showed a similar significant tendency to sign more frequently to the normal playback stimulation rather than to the reversed and the scrambled conditions. This effect was confirmed by a repeated measured one-way ANOVA against the three conditions **(p=0.0072)**, corroborated by a two-tailed paired t-test between condition normal and reversed (**p=0.0064**), normal versus scrambled **(p=0.021)**. No significant effect was found between reversed and scrambled (p=0.67) (**Figure** 7).

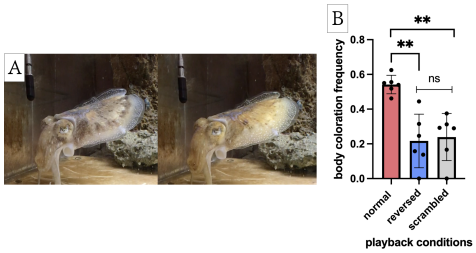

Fig. 8. Cuttlefish Sepia officinalis display more often vivid body colorations during the normal playback stimulation. **A**- During the playback, the same cuttlefish display two different body color at few time points interval (mottle followed by orange and black spot). **B**. Sepia officinalis show a robust tendency to display bright and rapidly shifting skin coloration during the normal stimulation as opposed to control (reversed and scrambled)

Finally, we collected data from the skin pattern with a GoPro camera fixed above the tank. We manually annotated the expression of communication skin patterns following the SAME method. We annotated communication displays in which the color/brightness of the body pattern changed vividly and rapidly. For instance, we would label a time window where the cuttlefish would exhibit bright orange pattern or vivid black point, or a traveling wave in response to the playback stimuli. We finally found that all cuttlefish expressed significantly more correlated high-contrast skin patterns during normal conditions (Figure 8) (**Supplementary video 5**). In Sepia officinalis, we also observed that in addition to expressing vivid skin patterning, cuttlefish also display specific behaviors and body patterns during the playback experiment such as lateral pupil contraction, eye and head movements, burying, swimming toward the hydrophone to touch the device, extending the tentacules as in a prey-catching attempt displaying "hunting arms", extension of the fourth arm associated with Zebra bands, change in body shape, and inking. We also observed recurrence of fin flipping in a stereotyped manner similar to the wave signs. In Sepia bandensis, we observed rapid changes in coloration (usually black), hunting arms (consisting of waving the first pair of arms on one side or the other), inking, swimming, body contraction, especially of the mantle, eyes and head movements.

Spectrotemporal analysis of the recorded waveforms. We visualized and plotted the seven traces corresponding to sign 1 'Up' recorded from a spontaneous sequence emitted by a female cuttlefish (**Figure 9A–G**). We computed their associated spectrograms up to 40 Hz (**Figure 9H–N**). We find a common peak of energy at about 15-20 Hz. We plotted the average across the frequencies of all traces (**Figure 9O**). We interpret the obtained power spectrum, representing the increase and decrease in power within the 10-30 Hz range, as a possible representation of the "Up" wave sign.

Discussion

In this study, we demonstrated that two species of cuttlefish exhibit comparable stereotyped 'arm wave signs' that can be

elicited by visual and vibratory displays. More specifically, we found that cuttlefish wave back significantly more to normal version of video stimuli displaying videos of themselves signing, rather than in a control version where the videos are upverted and showing cuttlefish not signing in Sepia bandensis. Furthermore, cuttlefish wave back to playback of traces of their own recorded signs displayed by a hydrophone and a speaker. We interpret those results as a first proof of concept that cuttlefish use the four arm wave signs as signals to interact and possibly to communicate with each other. In the following, we discuss relevant connections with the existing literature, address interpretational difficulties, and potential implications of our finding for multimodal cephalopod communication.

Meaning of the arm wave signs. Elucidating the meaning of those arm wave signs is a challenge inherent in this study. First, they could be domination signs. In fact, we observed that when a cuttlefish is waving, it usually places itself in front of the tank, and other cuttlefish tend to withdraw, as if there was the establishment of a hierarchy. However, every cuttlefish can elicit each type of signs, male or female, and their size did not appear to correlate with their propensity to sign. They could potentially occur as courtship displays, in line with their attractiveness and exaggeration (20, 77). Nonetheless, we observed that these signs can be expressed by juveniles who have not yet reached sexual maturity in both Sepia bandensis and Sepia officinalis. These signs could be aversive displays since they appear to be expressed to other cuttlefish in defensive context, potential predators (shrimps bigger in size than juveniles) and humans approaching the tank. They could express internal states and or/mood. This is possible since signs are sometimes spontaneously conveyed when there is no external stimulation. Signs could attract prey or be used to detect prey, because they are often exhibited in the close presence of live prey food. Furthermore, during both the visual experiment and the playback experiment, cuttlefish occasionally elicited other types of arm displays, like hunting arms or tentacule ejection for prey catching. The most plausible interpretation is that these signs are symbolic and can encrypt a variety of possible meanings depending on the associated behavioral contexts. We also found that the signs are expressed in correlation with other body patterns: dynamic skin coloration (passing cloud, orange, black spot, dark skin coloration, bright white coloration, zebra bands) change in body shape (body rounded), stereotyped fin flipping. We also observed that they exhibit other behavior simultaneously: inking, especially during the playback experiment, pupil contraction, head and eye movements, prey detection, burying, hiding behind rocks, swimming. Future studies should quantify those elicited observed behaviors with more precision by operationalizing further behavioral experiments. Those observations align with previous studies on behavioral responses to sound in cuttlefish (54). Both during the visual and playback experiments, juvenile Sepia bandensis expressed only the "up" and "crown" signs, despite the fact that we observed them displaying the other signs spontaneously outside the experiments. One would need to explore if this is correlated to their young age for instance. Deciphering the meaning of wave signs would require to establish specific correlations between arm wave signs, associated body patterns, and specific behavioral contexts of expression, in order to perform clustering and correlation analysis. Those methods are enabled and optimized by recent development of machine learning algorithms and methods used to quantify dynamic skin patterning (6, 76, 79, 80). We finally noticed that cuttlefish spontaneously display wave signs in complex long-lasting sequences and combine different types of signs with associated body patterns. Further explorations involving Markov models could enable one to decipher the meaning of signs in relation to specific behavioral contexts and individual differences (sex, size, age) (81). In this study, our objective was to demonstrate that these signs are used by cuttlefish to interact with each other and could constitute a multimodal communication display. We presented two films with random sequences of cuttlefish, males and females, displaying all types of signs, with their respective flipped control versions. We then inverted both images upside down. This manipulation is known to interfere with the semantic interpretation of the scene, while leaving all other image properties unaffected (82, 83). For example, the upside-down image allocates contrast to detail in a manner identical to that of the upright image; it also contains the same set of contours/objects/edges. For this reason, inversion represents a powerful tool for selectively targeting the higher-level representation of the image while sidestepping its low- level characteristics (84). This phenomenon is convincingly demonstrated by the Thatcher illusion (85), where gross distortions of the eye and mouth regions go perceptually unregistered when the face is upside down, but are readily available in the upright configuration. Similar effects can be demonstrated for natural scenes (86, 87). We found that cuttlefish respond significantly more to the normal version for both films (**Figure 2D**). This result is in favor of our hypothesis that wave signs carry semantic information, which can be extracted by the visual system of the cuttlefish.

Relation of our study with previous background literature on cuttlefish and cephalopods arm postures and movements. A case for cephalopod intraspecific communication?. Our visual and sound elicitation of arm wave signs was effective in two different species of cuttlefish, Sepia officinalis and Sepia bandensis. The two cohorts were never exposed to one another and were raised in different tanks so we discard any biais due to observational learning between the two species. We did not reinforce or condition the elicitation of signs with ant specific rewards or punishment. Sepia officinalis and Sepia bandensis display very similar and comparable wave signs. The results of our two behavioral experiments support the hypothesis that these signs are communication displays used to interact with each another. However, we also observed that they exhibit the signs to their prey shrimps, to humans, and to the introduction of specific objects into the tank. We also observed a display of similar signs in the cephalopod Sepiola atlantica interacting with a shrimp **(Supplementary video 6**).

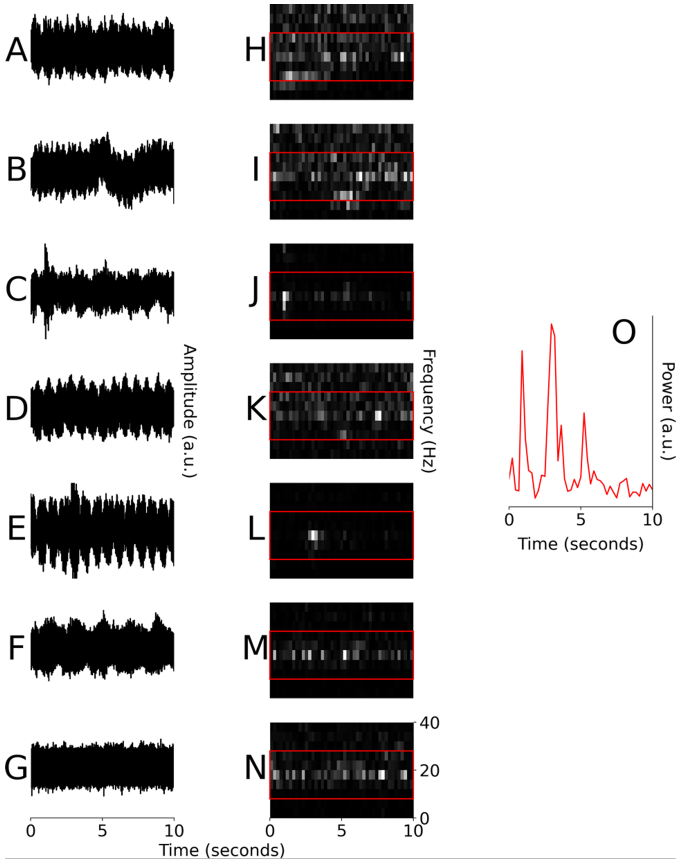

Fig. 9. Spectrotemporal content of recorded wave signs. We recorded seven samples of wave signs (**A**–**G**) using a hydrophone (see **Figure 3 A**–**C**). Corresponding spectrograms (**H**–**N**) indicated that information relevant to signing mostly lied within the 10–30 Hz range (indicated by red rectangles in **H**–**N**). When we average power across this frequency range and across samples, we obtain a slowly fluctuating power change (red trace in **O**) possibly reflecting the wave sign. We focused on spectrogram regions below 40 Hz (shown in **H**–**N**) because we recorded large power increases at 50 Hz and associated harmonics, which almost certainly reflected the mains power supply. In addition, existing literature on the characteristics of the lateral line and statocysts (41, 47, 54) points to this range as the most plausible carrier for information relating to biologically meaningful vibrations like those studied here.

In this section, we argue that these arm wave signs may be a signal shared between different species of cuttlefish and potentially be used as intraspecific and even interspecific display. First, it is likely that the list of the four arm wave signs will be extended, and studied along with other stereotyped arm wave signs already documented both in cuttlefish and other cephalopods. For example, Okamoto showed that another species of cuttlefish Sepia pharaonis also exhibits a very stereotyped and specific arm wave movement during hunting that they interpreted as a mimicking signal (11). Future research could also elucidate whether the fourth sign that we referred to as 'crown' in our experiment corresponds to the opening and extension of the arm crown in the exaggerated 'Umbrella pattern' during mating studied in Sepia latimanus (7). In Sepia officinalis, the 'fourth arm extension' is very well documented and 'spread of arms and web' is part of the reference signs known in this cuttlefish (7). Finally, a category of 'Arm wave' had been documented as posture in Sepia officinalis (8, 9) but we would need additional specifications on its specific features, to correlate potentially this category with one of our signs. This opens a potential for the development of an algorithm that would automatically label, track and categorize arm wave signs in cuttlefish to produce a uniform atlas of the different existing arm movements and postures and decipher their meaning and ecological context of expression. In squids, arm postures have been widely studied in the context of communication and camouflage. In Mather "squid dance" ethograms, the 'bad hair' display is to some extent comparable to our 'Up' cuttlefish, where the *'arms and tentacles are splayed equally, bent proximally toward the body without systematic spacing, held loosely and twisted'* (15). In the squid Sepiotheutis australis, Jantzen and al. described different postures and movements in the context of mating constitutive of a complex visual communication system (14). Very interestingly, in the squid, Mooney found that a specific frequency of sounds evokes stereotyped fin movements (55). It would be interesting to compare this fin flip movement with the one we evoked during our playback experiment. Our present study aligns with his findings, as well as those on cuttlefish behavior responses to sound by Samson (51, 54) and provides further argument to explore the differences and similarities between responses to specific frequencies between cephalopod species as suggested by Mooney (55). Our study is complementary to those previous findings in the way that we focused on a specific frequency bandwidth, at a fixed amplitude, corresponding to the specific waveform that most closely approximates the arm wave sign waveform, considering technical limitations.

The implication of our study as regards background literature in cephalopod bioacoustics. Following the assumption that the wave signs produce specific vibration in the water, we tested that the arm wave signs could be perceived through mechanoreception. The two candidate organs for low-frequency sensory perception in cuttlefish (around 15-35 Hz) are the lateral line and the statocysts (37, 39, 46, 47, 64, 70, 88). We emphasize that the position of the lateral line hair cells on the surface of the skin on the arms and head of the an-

imal constitutes a form-to-function argument in favor of our hypothesis, as well as the position of iridophores cells on the arms used for communication through light polarization (32–34, 36). During our playback experiments we also notice that cuttlefish contract one or two eyes. This suggests that the vibration generated could also stimulate the vestibular system (evoking the vestibulo ocular-reflex), understood here as the statocysts with statoliths enabling to maintain balance and orientation by stimulating the hair cells. Cephalopod statocyts have been proven to be receptive to low-frequency vibrations and act as a gravity detector (47, 50). Further study and exploration at the cellular and molecular levels should unravel if the arm wave signs are perceived through the lateral line, statocysts or both. In fact, perception of arm wave signs through statocyst stimulation is an equally relevant alternative assumption to lateral line stimulation to be explored. This postulate would be supported by electrophysiological evidence that statocysts in the Longfin squid detect low-frequency vibrations (20-1000 Hz) from predators and prey and for navigation (47, 50). Furthermore, Mooney highlights that, despite the fact that cephalopods do not make sounds, jet propulsion in squid produces low-frequency water flow with strong particle motion that could be used as cues during schoaling (47). Our results support this argument, all the more so that when displaying the crown sign, cuttlefish 'jet' in some manner. According to Kaifu, the lateral line hair cells working distance is one body length whereas statocyts are stimulated by whole body displacement at a larger working distance and are hence the receptors of sound per-se (42). During our playback experiments, the hydrophone and speaker were usually placed around one body length of the animal, close to the arms. However, further investigation could parametrize the exact distance of projection to de-correlate the participation of the lateral line/ statocysts in perceiving the arm wave signs. Alternative neural correlates could be implied in the perception of the wave signs. Other types of sensory cells, such as chemoreceptors in the arms, may play a role in this multimodal communication display. It would be necessary to elucidate whether the hair cells of the lateral line of the cuttlefish also integrate chemical cues, as it has been established recently in the zebrafish (89). In addition, cuttlefish exhibit a stereotyped "fin flipping" display simultaneously or independently of wave signs. Possibly, the wave signs could also stimulate the hair cells disposed along the fins of the animal (90). Previously, there was no specific evidence that cuttlefish could communicate with each other by emitting specific vibrational signals, nor was there specific evidence of involvement of the lateral line and statocysts for intraspecies communication in cephalopods. In 1991, Budelmann performed preliminary behavioral experiments that revealed that the ability of cuttlefish to catch shrimp in complete darkness most likely depends on the functioning of epidermal lines (39). In cephalopods, schooling behavior is attested in Sepia officinalis (91). However, this study does not detail which sensory modality is involved in this behavior nor mention the potential role played by the lateral line. In 2014, York showed that the lateral line is used as a complementary sensory modality system to aid vision in successful predator evasion for the brief squid Lolliguncula brevis (67). Squids and cuttlefish were shown to use the lateral line for the detection of prey (39). Nonetheless, it is well known and supported by extensive scientific evidence that cephalopods and cuttlefish possess a wide repertoire of behavioral responses to sounds that could stimulate the lateral / statocysts or both (38, 42, 43, 45–47, 49–52). Finally, could those arm wave signs be used as auto-communication signals, as in a form of echolocation? Future experiments could test this hypothesis considering that the lateral line is used to detect and localize prey and that we observed the arm wave signs displayed in sequence with the hunting arms.

Limitations in terms of stimuli presentation. A first limitation of our study is that we projected only one type of arm wave sign, the "up" sign in the cuttlefish Sepia officinalis, recording from one female adult cuttlefish. In Sepia bandensis, we captured and playback the 'up' and 'crown' sign. Future investigations should record various traces of different types of signs, in different behavioral conditions, for different animals, at different stages of life. We also introduced a potential bias by presenting a recomposed sequence that could disrupt a potential biological meaning. Furthermore, it is also likely that when cuttlefish sign back, they could expect an answer in a loop, as in a dialogue. Do cuttlefish wave back at the vibration of the recorded arm wave or more generally to a low-frequency bandwidth captured by the hydrophone? To elucidate this problem, we could envision quantifying and measuring more specifically the vibrations emitted by the arm wave signs, to be able to distinguish between signatures of movements of the water, vibrational traces of the animal moving (swimming for instance), background noise, and the arm wave itself. We made a step forward in that direction by analyzing the power spectrum of the arm wave and found that a specific trace fluctuating between 10-35 Hz could be the signature of the wave sign (**Figure 9**). Although a structure appeared, the use of more sophisticated equipment and reduction of the background noise should lead to the generation of better traces corresponding to each wave sign in future investigations. Nonetheless, our study demonstrates that the display of low-frequency vibrations at around 20 Hz can elicit the arm wave signs, with a hydrophone and a speaker, in both cuttlefish species. Finally, we conducted all our experiments on mechanoreception of the arm wave sign in the daylight. Is there an effect of chronobiology on the perception modality? For instance, it is assumed that the lateral line is very useful for animals in turbid waters for detecting prey (92). Using mechanoreception is efficient in dark environments. Future studies could test the effect of the absence of light on the elicitation of arm wave signs. We performed our experiment in a relatively small closed tank compared to wild conditions, the projected vibrations could have been distorted and reverberated (93–95). Hu also warns that the flow of water can cause artifacts in the recordings over the hydrophone by creating vortex shedding fluctuating pressure around the hydrophone, which is detected by the hydrophone and appears as noise in the recordings (40, 95). However, in a closed tank, the flow

of the water is relatively slight, but we could have improved our protocol by placing the hydrophone in a sheltered area and, even better, by using multiple hydrophones. A future experimental set-up could consist of recording the vibration emitted by the arm wave signs with more refined equipment, such as a laser Doppler anemometer.

Second, we designed two variants of the playback experiment. With the common cuttlefish Sepia officinalis, we decided to let the animals evolve in their natural home tank environment to prevent potential biais due to conditioning and stress. We let other cuttlefish and prey evolve around the animal, but control for the specific effect of the playback display by designing two specific controls: a reversed and a scrambled trace. On the other hand, for cuttlefish Sepia bandensis, we completely isolated the tested animal in a specific tank, where a speaker had been placed in advance to prevent the animal from noticing the introduction of a specific object into the tank. We let the animal acclimate for 30 minutes to avoid potential stress. In fact, we noticed that when we moved the animal in the test tank, some of them would elicit a crown sign and dark skin coloration. We found similar results with both variants of the playback experiment setup.

Conclusion

In this study, we introduced four different 'arm wave signs' in the common cuttlefish and their variant in cuttlefish Sepia bandensis. We demonstrated, with two behavioral non-invasive experiments, that they are communication signals perceived through vision and mechanoreception. Arm wave signs can be combined into long sequences with many permutations, with structure and meaning that are open for future exploration. They are also correlated with the expression of specific body patterns, providing further potential for forthcoming research. We found that cuttlefish respond to visual displays of cuttlefish executing the arm wave displays by waving back. We interpreted this result as a proof of concept that they communicate visually, the effect being weakened with a control manipulation (upside-down inversion) meant to interfere with the semantic content of the stimulus. We demonstrated that cuttlefish respond to both a hydrophone and a speaker emitting low-frequency vibrations corresponding to the traces of recorded wave signs. Our new result on communication with arm wave signs opens up novel possibilities for understanding vibration-mediated communication through the lateral line and/or the statocysts in a cephalopod species. Overall, our study posits a convergent evolution for the role of the lateral line and/or statocysts in communication between cephalopods, fish, and amphibians.

Supplementary materials and data availability. Supplementary materials including supplementary videos, a subset of data that allow replication of the results, and coding scripts are available in an open access Mendeley Data repository online: "Cuttlefish interact with multimodal arm wave sign displays", Mendeley Data, V4, doi: 10.17632/f3sp55762b.4

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Competing interests. The authors declare that they have no competing interests.

Bibliography.

1. R. T. Hanlon, J. B. Messenger, and John Zachary Young. Adaptive coloration in young cuttlefish (sepia officinalis l.): the morphology and development of body patterns and their relation to behaviour. 320(1200):437–487. doi: 10.1098/rstb.1988.0087.
2. Chuan-Chin Chiao and Roger T. Hanlon. Cuttlefish camouflage: visual perception of size, contrast and number of white squares on artificial checkerboard substrata initiates disruptive coloration. 204(12):2119–2125. ISSN 0022-0949. doi: 10.1242/jeb.204.12.2119.
3. Francesca Gherardi Luciana Borrelli. A catalogue of body patterning in cephalopoda. Type: text.
4. Alexandra Barbosa, Lydia M. Mäthger, Kendra C. Buresch, Jennifer Kelly, Charles Chubb, Chuan-Chin Chiao, and Roger T. Hanlon. Cuttlefish camouflage: the effects of substrate contrast and size in evoking uniform, mottle or disruptive body patterns. 48(10):1242–1253. ISSN 0042-6989. doi: 10.1016/j.visres.2008.02.011.
5. S. Zylinski, M. J. How, D. Osorio, R. T. Hanlon, and N. J. Marshall. To be seen or to hide: Visual characteristics of body patterns for camouflage and communication in the australian giant cuttlefish sepia apama. 177(5):681–690. ISSN 0003-0147. doi: 10.1086/659626.
6. Daniel Osorio, François Ménager, Christopher W. Tyler, and Anne-Sophie Darmaillacq. Multi-level control of adaptive camouflage by european cuttlefish. 32(11):2556–2562.e2. ISSN 1879-0445. doi: 10.1016/j.cub.2022.04.030.
7. Roger T. Hanlon and John B. Messenger. *Cephalopod Behaviour*. Cambridge University Press, 2 edition, . ISBN 978-0-521-89785-3. doi: 10.1017/9780511843600.
8. Roger T. Hanlon and John B. Messenger. *Cephalopod behaviour*. Cephalopod behaviour. Cambridge University Press, . ISBN 978-0-521-42083-9 978-0-521-64583-6.
9. J. B. Messenger. Cephalopod chromatophores: neurobiology and natural history. 76(4): 473–528. ISSN 1464-7931. doi: 10.1017/s1464793101005772.
10. A. Packard. Cephalopods and fish: The limits of convergence. 47(2):241–307. ISSN 1469-185X. doi: 10.1111/j.1469-185X.1972.tb00975.x.
11. Kohei Okamoto, Haruhiko Yasumuro, Akira Mori, and Yuzuru Ikeda. Unique arm-flapping behavior of the pharaoh cuttlefish, sepia pharaonis: putative mimicry of a hermit crab. 35 (3):307–311. ISSN 0289-0771. doi: 10.1007/s10164-017-0519-7.
12. M. D. Norman, J. Finn, and T. Tregenza. Dynamic mimicry in an indo-malayan octopus. 268 (1478):1755–1758. ISSN 0962-8452. doi: 10.1098/rspb.2001.1708.
13. W. H. Sauer, M. J. Roberts, M. R. Lipinski, M. J. Smale, R. T. Hanlon, D. M. Webber, and R. K. O'Dor. Choreography of the squid's "nuptial dance". 192(2):203–207. ISSN 0006-3185. doi: 10.2307/1542714.
14. Troy M. Jantzen and Jon N. Havenhand. Reproductive behavior in the squid sepioteuthis australis from south australia: interactions on the spawning grounds. 204(3):305–317. ISSN 0006-3185. doi: 10.2307/1543601.
15. Jennifer A. Mather, Ulrike Griebel, and Ruth A. Byrne. Squid dances: an ethogram of postures and actions of *Sepioteuthis* sepioidea squid with a muscular hydrostatic system. 43(1):45–61. ISSN 1023-6244, 1029-0362. doi: 10.1080/10236241003660771.
16. SHELLEY A. Adamo and R. T. Hanlon. Do cuttlefish (cephalopoda) signal their intentions to conspecifics during agonistic encounters? 52(1):73–81. ISSN 0003-3472. doi: 10.1006/anbe.1996.0153.
17. Jennifer Mather. Cephalopod skin displays: from concealment to communication.
18. Keri V. Langridge. Cuttlefish use startle displays, but not against large predators. 77(4): 847–856. ISSN 0003-3472. doi: 10.1016/j.anbehav.2008.11.023.
19. David Scheel, Peter Godfrey-Smith, and Matthew Lawrence. Signal use by octopuses in agonistic interactions. 26. doi: 10.1016/j.cub.2015.12.033.
20. Alexandra K. Schnell, Carolynn L. Smith, Roger T. Hanlon, Karina C. Hall, and Robert Harcourt. Cuttlefish perform multiple agonistic displays to communicate a hierarchy of threats. 70(10):1643–1655. ISSN 1432-0762. doi: 10.1007/s00265-016-2170-7.
21. Martin J. How, Mark D. Norman, Julian Finn, Wen-Sung Chung, and N. Justin Marshall. Dynamic skin patterns in cephalopods. 8. ISSN 1664-042X.

22. F. Paul DiMarco and Roger T. Hanlon. Agonistic behavior in the squid loligo plei (loliginidae, teuthoidea): Fighting tactics and the effects of size and resource value. 103(2):89–108. ISSN 1439-0310. doi: 10.1111/j.1439-0310.1997.tb00010.x.
23. Peter Morse and Christine L. Huffard. Tactical tentacles: New insights on the processes of sexual selection among the cephalopoda. 10, . ISSN 1664-042X.
24. Peter Morse and Christine Huffard. Tactile social recognition in octopuses, . Place: Rochester, NY Type: SSRN Scholarly Paper.
25. J. G. Boal and S. E. Marsh. Social recognition using chemical cues in cuttlefish (*Sepia* officinalis linnaeus, 1758). 230(2):183–192. ISSN 0022-0981. doi: 10.1016/S0022-0981(98)00068-9.
26. Jean G. Boal, Krista N. Prosser, Johanna B. Holm, Tiffany L. Simmons, Robert E. Haas, and Gregg T. Nagle. Sexually mature cuttlefish are attracted to the eggs of conspecifics. 36(8):834–836, . ISSN 1573-1561. doi: 10.1007/s10886-010-9816-0.
27. Scott F. Cummins, Jean G. Boal, Kendra C. Buresch, Chitraporn Kuanpradit, Prasert Sobhon, Johanna B. Holm, Bernard M. Degnan, Gregg T. Nagle, and Roger T. Hanlon. Extreme aggression in male squid induced by a β-MSP-like pheromone. 21(4):322–327. ISSN 0960-9822. doi: 10.1016/j.cub.2011.01.038.
28. Roy L. Caldwell, Richard Ross, Arcadio Rodaniche, and Christine L. Huffard. Behavior and body patterns of the larger pacific striped octopus. 10(8):e0134152. ISSN 1932-6203. doi: 10.1371/journal.pone.0134152.
29. Alison J King, Shelley A Adamo, and Roger T Hanlon. Squid egg mops provide sensory cues for increased agonistic behaviour between male squid. 66(1):49–58. ISSN 0003-3472. doi: 10.1006/anbe.2003.2197.
30. Kendra C. Buresch, Jean G. Boal, Jamie Knowles, Jennifer Debose, Amy Nichols, Ali Erwin, Sherry D. Painter, Gregg T. Nagle, and Roger T. Hanlon. Contact chemosensory cues in egg bundles elicit male-male agonistic conflicts in the squid loligo pealeii. 29(3):547–560. ISSN 0098-0331. doi: 10.1023/a:1022846603591.
31. James B. Wood, Kelly E. Pennoyer, and Charles D. Derby. Ink is a conspecific alarm cue in the caribbean reef squid, *Sepioteuthis* sepioidea. 367(1):11–16. ISSN 0022-0981. doi: 10.1016/j.jembe.2008.08.004.
32. N. Shashar, P. Rutledge, and T. Cronin. Polarization vision in cuttlefish in a concealed communication channel? 199:2077–2084, . ISSN 1477-9145. doi: 10.1242/jeb.199.9.2077.
33. N. Shashar, R. Hagan, J. G. Boal, and R. T. Hanlon. Cuttlefish use polarization sensitivity in predation on silvery fish. 40(1):71–75, . ISSN 0042-6989. doi: 10.1016/s0042-6989(99)00158-3.
34. Jean Boal, Nadav Shashar, Melissa Grable, Ellis Loew, Roger Hanlon, and Katrina Vaughan. Behavioral evidence for intraspecific signaling with achromatic and polarized light by cuttlefish (mollusca: Cephalopoda). 141(7):837–861, . ISSN 0005-7959, 1568-539X. doi: 10.1163/1568539042265662.
35. Lydia M. Mäthger and Roger T. Hanlon. Anatomical basis for camouflaged polarized light communication in squid. 2(4):494. doi: 10.1098/rsbl.2006.0542.
36. Lydia M. Mäthger, Nadav Shashar, and Roger T. Hanlon. Do cephalopods communicate using polarized light reflections from their skin? 212:2133–2140. ISSN 0022-0949. doi: 10.1242/jeb.020800.
37. Bernd U. Budelmann and Horst Bleckmann. A lateral line analogue in cephalopods: water waves generate microphonic potentials in the epidermal head lines ofSepia andLolliguncula. 164(1):1–5. ISSN 1432-1351. doi: 10.1007/BF00612711.
38. A. Packard, H. E. Karlsen, and O. Sand. Low frequency hearing in cephalopods. 166(4):501–505. ISSN 1432-1351. doi: 10.1007/BF00192020.
39. Bernd Budelmann, U Riese, and Horst Bleckmann. *Structure, function, biological significance of the cuttlefish 'lateral lines'*.
40. Marian Y. Hu, Hong Young Yan, Wen-Sung Chung, Jen-Chieh Shiao, and Pung-Pung Hwang. Acoustically evoked potentials in two cephalopods inferred using the auditory brainstem response (ABR) approach. 153(3):278–283. ISSN 1095-6433. doi: 10.1016/j.cbpa.2009.02.040.
41. Spogmai Komak, Jean G. Boal, Ludovic Dickel, and Bernd U. Budelmann. Behavioural responses of juvenile cuttlefish (sepia officinalis) to local water movements. 38(2):117–125. ISSN 1023-6244. doi: 10.1080/10236240500139206.
42. Kenzo Kaifu, Susumu Segawa, and Kotaro Tsuchiya. Behavioral responses to underwater sound in the small benthic octopus \textlessl\textgreaterOctopus ocellatus\textless/i\textgreater. 34(4):266–273, . doi: 10.3135/jmasj.34.266.
43. Kenzo Kaifu, Tomonari AKAMATSU, and Susumu SEGAWA. Underwater sound detection by cephalopod statocyst. 74:781–786, . doi: 10.1111/j.1444-2906.2008.01589.x.
44. Kenzo Kaifu, Tomonari Akamatsu, and Susumu Segawa. Preliminary evaluation of underwater sound detection by the cephalopod statocyst using a forced oscillation model. 32(6):255–260, . doi: 10.1250/ast.32.255.
45. Marta Solé, Marc Lenoir, José-Manuel Fortuño, Mike van der Schaar, and Michel André. A critical period of susceptibility to sound in the sensory cells of cephalopod hatchlings. 7(10):bio033860, . ISSN 2046-6390. doi: 10.1242/bio.033860.
46. Michel André, Marta Solé, Marc Lenoir, Mercè Durfort, Carme Quero, Alex Mas, Antoni Lombarte, Mike van der Schaar, Manel López-Bejar, Maria Morell, Serge Zaugg, and Ludwig Houégnigan. Low-frequency sounds induce acoustic trauma in cephalopods. 9(9):489–493. ISSN 1540-9309. doi: 10.1890/100124.
47. T. Aran Mooney, Roger T. Hanlon, Jakob Christensen-Dalsgaard, Peter T. Madsen, Darlene R. Ketten, and Paul E. Nachtigall. Sound detection by the longfin squid (loligo pealeii) studied with auditory evoked potentials: sensitivity to low-frequency particle motion and not pressure. 213(21):3748–3759, . ISSN 0022-0949. doi: 10.1242/jeb.048348.
48. Martin Moynihan. Why are cephalopods deaf? 125(3):465–469. ISSN 0003-0147.
49. Roger T. Hanlon. Why cephalopods are probably not "deaf". 129(2):312–317. ISSN 0003-0147. doi: 10.1086/284637.
50. T. Aran Mooney, Maya Yamato, and Brian K. Branstetter. Hearing in cetaceans: from natural history to experimental biology. 63:197–246, . ISSN 0065-2881. doi: 10.1016/B978-0-12-394282-1.00004-1.
51. Julia Samson, Aran Mooney, Sander Gussekloo, and Roger Hanlon. A brief review of cephalopod cephalopod behavioral responses to sound. In *Advances in experimental medicine and biology*, volume 875. . ISBN 978-1-4939-2980-1. doi: 10.1007/978-1-4939-2981-8_120.
52. Marta Solé, Kenzo Kaifu, T. Aran Mooney, Sophie L. Nedelec, Frédéric Olivier, Andrew N. Radford, Mirella Vazzana, Matthew A. Wale, Jayson M. Semmens, Stephen D. Simpson, Giuseppa Buscaino, Anthony Hawkins, Natacha Aguilar de Soto, Tomoari Akamatsu, Laurent Chauvaud, Ryan D. Day, Quinn Fitzgibbon, Robert D. McCauley, and Michel André. Marine invertebrates and noise. 10, . ISSN 2296-7745.
53. S. Dijkgraaf. Sound reception in the dogfish. 197:93–94. ISSN 0028-0836. doi: 10.1038/197093a0.
54. Julia E. Samson, T. Aran Mooney, Sander W. S. Gussekloo, and Roger T. Hanlon. Graded behavioral responses and habituation to sound in the common cuttlefish sepia officinalis. 217:4347–4355, . ISSN 1477-9145. doi: 10.1242/jeb.113365.
55. T. Aran Mooney, Julia E. Samson, Andrea D. Schlunk, and Samantha Zacarias. Loudness-dependent behavioral responses and habituation to sound by the longfin squid (doryteuthis pealeii). 202(7):489–501, . ISSN 1432-1351. doi: 10.1007/s00359-016-1092-1.
56. Kyle C. Newton, Dovi Kacev, Simon R. O. Nilsson, Allison L. Saettele, Sam A. Golden, and Lavinia Sheets. Lateral line ablation by ototoxic compounds results in distinct rheotaxis profiles in larval zebrafish. 6(1):84. ISSN 2399-3642. doi: 10.1038/s42003-023-04449-2.
57. John Montgomery, Horst Bleckmann, and Sheryl Coombs. Sensory ecology and neuroethology of the lateral line. In Sheryl Coombs, Horst Bleckmann, Richard R. Fay, and Arthur N. Popper, editors, *The Lateral Line System*, Springer Handbook of Auditory Research, pages 121–150. Springer. ISBN 978-1-4614-8851-4. doi: 10.1007/2506_2013_17.
58. J. C. Montgomery and D. Bodznick. An adaptive filter that cancels self-induced noise in the electrosensory and lateral line mechanosensory systems of fish. 174(2):145–148. ISSN 0304-3940. doi: 10.1016/0304-3940(94)90007-8.
59. M. Satou, H.-A. Takeuchi, J. Nishii, M. Tanabe, S. Kitamura, N. Okumoto, and M. Iwata. Behavioral and electrophysiological evidences that the lateral line is involved in the inter-sexual vibrational communication of the himé salmon (landlocked red salmon, oncorhynchus nerka). 174(5):539–549. ISSN 1432-1351. doi: 10.1007/BF00217373.
60. Mana Mirjany, Thomas Preuss, and Donald S. Faber. Role of the lateral line mechanosensory system in directionality of goldfish auditory evoked escape response. 214(20):3358–3367. ISSN 0022-0949. doi: 10.1242/jeb.052894.
61. Lourdes Martínez Medina, Constantino Macías Garcia, Amira Flores Urbina, Javier Manjarrez, and Alejandro Moyaho. Female vibration discourages male courtship behaviour in the amarillo fish (girardinichthys multiradiatus). 100:163–168. ISSN 1872-8308. doi: 10.1016/j.beproc.2013.09.007.
62. Julie M. Butler and Karen P. Maruska. The mechanosensory lateral line is used to assess opponents and mediate aggressive behaviors during territorial interactions in an african cichlid fish. 218:3284–3294, . ISSN 1477-9145. doi: 10.1242/jeb.125948.
63. Julie M. Butler and Karen P. Maruska. The mechanosensory lateral line system mediates activation of socially-relevant brain regions during territorial interactions. 10:93, . ISSN 1662-5153. doi: 10.3389/fnbeh.2016.00093.
64. Horst Bleckmann and Bernd Budelmann. On the senses of the cuttlefish. a lateral line system in cephalopods. 3:8.
65. H. Bleckmann. Peripheral and central processing of lateral line information. 194(2):145–158. ISSN 0340-7594. doi: 10.1007/s00359-007-0282-2.
66. Shelley A. Adamo and Kathy J. Weichelt. Field observations of schooling in the oval squid, sepioteuthis lessoniana (lesson, 1830). 65(3):377–380. ISSN 0260-1230. doi: 10.1093/mollus/65.3.377.
67. Carly A. York and Ian K. Bartol. Lateral line analogue aids vision in successful predator evasion for brief squid *Lolliguncula* brevis. page jeb.102871. ISSN 1477-9145, 0022-0949. doi: 10.1242/jeb.102871.
68. Peter K. McGregor, Clive K. Catchpole, Torben Dabelsteen, J. Bruce Falls, Leonida Fusani, H. Carl Gerhardt, Francis Gilbert, Andrew G. Horn, Georg M. Klump, Donald E. Kroodsma, Marcel M. Lambrechts, Karen E. McComb, Douglas A. Nelson, Irene M. Pepperberg, Laurene Ratcliffe, William A. Searcy, and Daniel M. Weary. Design of playback experiments: The thornbridge hall NATO ARW consensus. pages 1–9. Springer US. ISBN 978-1-4419-3224-2 978-1-4757-6203-7. doi: 10.1007/978-1-4757-6203-7_1.
69. Sarah B. Douglas and Daniel J. Mennill. A review of acoustic playback techniques for studying avian vocal duets. 81(2):115–129. ISSN 0273-8570.
70. T. Aran Mooney, Roger Hanlon, Peter T. Madsen, Jakob Christensen-Dalsgaard, Darlene R. Ketten, and Paul E. Nachtigall. Potential for sound sensitivity in cephalopods. 730:125–128, . ISSN 0065-2598. doi: 10.1007/978-1-4419-7311-5_28.
71. Graziano Fiorito, Andrea Affuso, Jennifer Basil, Alison Cole, Paolo de Girolamo, Livia D'Angelo, Ludovic Dickel, Camino Gestal, Frank Grasso, Michael Kuba, Felix Mark, Daniela Melillo, Daniel Osorio, Kerry Perkins, Giovanna Ponte, Nadav Shashar, David Smith, Jane Smith, and Paul L. R. Andrews. Guidelines for the care and welfare of cephalopods in research -a consensus based on an initiative by CephRes, FELASA and the boyd group. 49(2):1–90. ISSN 1758-1117. doi: 10.1177/0023677215580006.
72. W. M. S. Russell. The three rs: past, present and future. 14(4):279–286. ISSN 0962-7286, 2054-1538. doi: 10.1017/S0962728600029596.
73. Dylan M. Jones, Christopher Miles, and Jean Page. Disruption of proofreading by irrelevant speech: Effects of attention, arousal or memory? 4(2):89–108. ISSN 1099-0720. doi: 10.1002/acp.2350040203.
74. Mary F. Howard and David Poeppel. Discrimination of speech stimuli based on neuronal response phase patterns depends on acoustics but not comprehension. 104(5):2500–2511. ISSN 0022-3077. doi: 10.1152/jn.00251.2010.
75. L. N. Piotrowski and F. W. Campbell. A demonstration of the visual importance and flexibility of spatial-frequency amplitude and phase. 11(3):337–346. ISSN 0301-0066. doi: 10.1068/p110337.
76. Theodosia Woo, Xitong Liang, Dominic A. Evans, Olivier Fernandez, Friedrich Kretschmer, Sam Reiter, and Gilles Laurent. The dynamics of pattern matching in camouflaging cuttlefish. 619(7968):122–128. ISSN 1476-4687. doi: 10.1038/s41586-023-06259-2. Publisher: Nature Publishing Group.
77. Nikolaas Tinbergen. *The Study of Instinct*. Pygmalion Press, an imprint of Plunkett Lake Press.
78. Deirdre Barrett. *Supernormal stimuli*. W.W. Norton & Co. ISBN 978-0-393-06848-1.

79. Sam Reiter, Philipp Hülsdunk, Theodosia Woo, Marcel A. Lauterbach, Jessica S. Eberle, Leyla Anne Akay, Amber Longo, Jakob Meier-Credo, Friedrich Kretschmer, Julian D. Langer, Matthias Kaschube, and Gilles Laurent. Elucidating the control and development of skin patterning in cuttlefish. 562(7727):361–366. ISSN 1476-4687. doi: 10.1038/s41586-018-0591-3.
80. Sophie Cohen-Bodénès and Peter Neri. State-dependent dynamics of cuttlefish mantle activity. 227(14):jeb247457. ISSN 0022-0949. doi: 10.1242/jeb.247457.
81. Yossi Yovel and Oded Rechavi. AI and the doctor dolittle challenge. 33(15):R783–R787. ISSN 1879-0445. doi: 10.1016/j.cub.2023.06.063.
82. Robert K. Yin. Looking at upside-down faces. 81(1):141–145. ISSN 0022-1015. doi: 10.1037/h0027474.
83. Tim Valentine. Upside-down faces: A review of the effect of inversion upon face recognition. 79(4):471–491. ISSN 2044-8295. doi: 10.1111/j.2044-8295.1988.tb02747.x.
84. Dirk B. Walther, Eamon Caddigan, Li Fei-Fei, and Diane M. Beck. Natural scene categories revealed in distributed patterns of activity in the human brain. 29(34):10573–10581. ISSN 0270-6474, 1529-2401. doi: 10.1523/JNEUROSCI.0559-09.2009.
85. Peter Thompson. Margaret thatcher: A new illusion. 9(4):483–484. ISSN 1468-4233. doi: 10.1068/p090483.
86. Todd A. Kelley, Marvin M. Chun, and Kao-Ping Chua. Effects of scene inversion on change detection of targets matched for visual salience. 3(1):1. ISSN 1534-7362. doi: 10.1167/3.1.1.
87. Jochem W. Rieger, Christoph Reichert, Karl R. Gegenfurtner, Toemme Noesselt, Christoph Braun, Hans-Jochen Heinze, Rudolf Kruse, and Hermann Hinrichs. Predicting the recognition of natural scenes from single trial MEG recordings of brain activity. 42(3):1056–1068. ISSN 1053-8119. doi: 10.1016/j.neuroimage.2008.06.014.
88. H. Bleckmann, T. Breithaupt, R. Blickhan, and J. Tautz. The time course and frequency content of hydrodynamic events caused by moving fish, frogs, and crustaceans. 168(6): 749–757. ISSN 1432-1351. doi: 10.1007/BF00224363.
89. Laura Desban, Julian Roussel, Olivier Mirat, François-Xavier Lejeune, Ludovic Keiser, Nicolas Michalski, and Claire Wyart. Lateral line hair cells integrate mechanical and chemical cues to orient navigation. Pages: 2022.08.31.505989 Section: New Results.
90. William M. Kier, John B. Messenger, and Jaleel A. Miyan. Short communication mechanoreceptors in the fins of the cuttlefish, sepia officinalis. 119(1):369–373. ISSN 0022-0949. doi: 10.1242/jeb.119.1.369.
91. Christian Drerup and Gavan M. Cooke. Shoaling behaviour in the european cuttlefish sepia officinalis. 127(12):1101–1108. ISSN 1439-0310. doi: 10.1111/eth.13226.
92. Alice Goerger. *Ecologie visuelle de la seiche: effets de la turbidité sur la survie, le développement et la reproduction (SEDIMENT)*.
93. Peter H. Rogers, Anthony D. Hawkins, Arthur N. Popper, Richard R. Fay, and Michael D. Gray. Parvulescu revisited: Small tank acoustics for bioacousticians. In Arthur N. Popper and Anthony Hawkins, editors, *The Effects of Noise on Aquatic Life II*, Advances in Experimental Medicine and Biology, pages 933–941. Springer. ISBN 978-1-4939-2981-8. doi: 10.1007/978-1-4939-2981-8_115.
94. Arthur N. Popper and Anthony D. Hawkins. An overview of fish bioacoustics and the impacts of anthropogenic sounds on fishes. 94(5):692–713. ISSN 1095-8649. doi: 10.1111/jfb.13948.
95. Christine Erbe, Micheal L. Dent, William L. Gannon, Robert D. McCauley, Heinrich Römer, Brandon L. Southall, Amanda L. Stansbury, Angela S. Stoeger, and Jeanette A. Thomas. The effects of noise on animals. In Christine Erbe and Jeanette A. Thomas, editors, *Exploring Animal Behavior Through Sound: Volume 1: Methods*, pages 459–506. Springer International Publishing. ISBN 978-3-030-97540-1. doi: 10.1007/978-3-030-97540-1_13.